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Reproductive Cycle of the New Zealand Geoduck, *Panopea zelandica,* in Two North Island Populations

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Abstract. The reproductive cycle of the New Zealand geoduck, *Panopea zelandica* (Quoy & Gaimard, 1835), was studied over a 22 month period at two sites in northern New Zealand: Kennedy Bay, Coromandel, and Shelly Bay, Wellington. Standard histological analysis, measures of oocyte diameters, and gonadosomatic indices (GSIs) were used to describe the timing of gametogenic development and spawning. Sex ratios and size at sexual maturity were also assessed for both populations. Gametogenesis in both populations began in late autumn, with spawning beginning during spring in Kennedy Bay and in late summer in Shelly Bay. The difference in the timing of spawning was attributed to latitudinal gradients in temperature as both populations spawned when water temperatures reached 15°C approximately. Monthly mean oocyte values and GSIs closely followed the patterns evident in the histological analysis of the reproductive cycle. However, monthly mean number of eggs/follicle indicated that a small amount of spawning may begin earlier than indicated by histology. Sex ratios were equal in Shelly Bay, but there were significantly more males than females in Kennedy Bay. This was attributed to a large cohort of small males present in Kennedy Bay. Males in both populations matured earlier than females. Whether geoducks are protandric or the sexes have different growth needs to be investigated. The data presented here suggest that GSIs may be of use to marine farmers wanting a quick and easy method for assessing the reproductive state of potential broodstock.

INTRODUCTION

Fisheries for the geoduck, *Panope abrupta* (Conrad, 1849), in northwest America began in the 1970s (Shaul & Goodwin, 1982). It is now the most important clam fishery on the Pacific Coast (Campbell et al., 1998). The average annual ex-vessel value of geoducks harvested from 1990 to 1998 in Puget Sound, Washington, was US$14 million (Hoffman et al., 2000). By 1995, the British Columbian fishery had grown to a value of C$42.5 million (Hand et al., 1998). A small experimental fishery for the native New Zealand geoduck, *P. zelandica* (Quoy & Gaimard, 1835), began in 1988. However, this was restricted to one operation in one part of Golden Bay, Nelson (Breen et al., 1991). The fishery was closed in the early 1990s. Because of the large markets that exist throughout Asia for the North American geoduck, there has been renewed interest in commercially exploiting *P. zelandica,* either through natural harvesting or aquaculture.

Investigation of the seasonal reproductive cycle of any marine bivalve is essential for developing management strategies for potential fisheries (Shaw, 1965; Manzi et al., 1985; Sbrenna & Campioni, 1994), and for the development of aquaculture, as the successful hatchery-rearing of a species is dependent on a solid knowledge of the reproductive cycle of potential broodstock. Except for the preliminary work of Breen et al. (1991), nothing is known of the reproductive biology of this species.

Traditionally, histological techniques are the most reliable method of determining reproductive development (Eversole et al., 1980; Manzi et al., 1985; Hooker & Creese, 1995; Gribben et al., 2001). Histological sections can be used for both qualitative and quantitative analysis of gametogenic development, typically using measures of oocyte size (e.g., Kennedy & Battle, 1964; Heffernan & Walker, 1989; Kanti et al., 1993; Gribben et al., 2001). Often, however, marine farmers and fisheries managers require the development of quick methods for determining the reproductive state of broodstock. Gonadosomatic Indices (GSIs) have been used with some success in determining the reproductive state of bivalves when compared with histological stagings (e.g., Ansell et al., 1980; Eversole et al., 1984; Fritz, 1991). Generally, GSIs that utilize wet-weight and dry-weight ratios are the simplest and quickest to compile.

This paper describes the reproductive cycle of the geoduck, *P. zelandica,* from two populations separated latitudinally by ~ 600 km in northern New Zealand using histological techniques. The timing of reproductive development and spawning has also been identified. Analysis of oocyte diameters from the histologically prepared

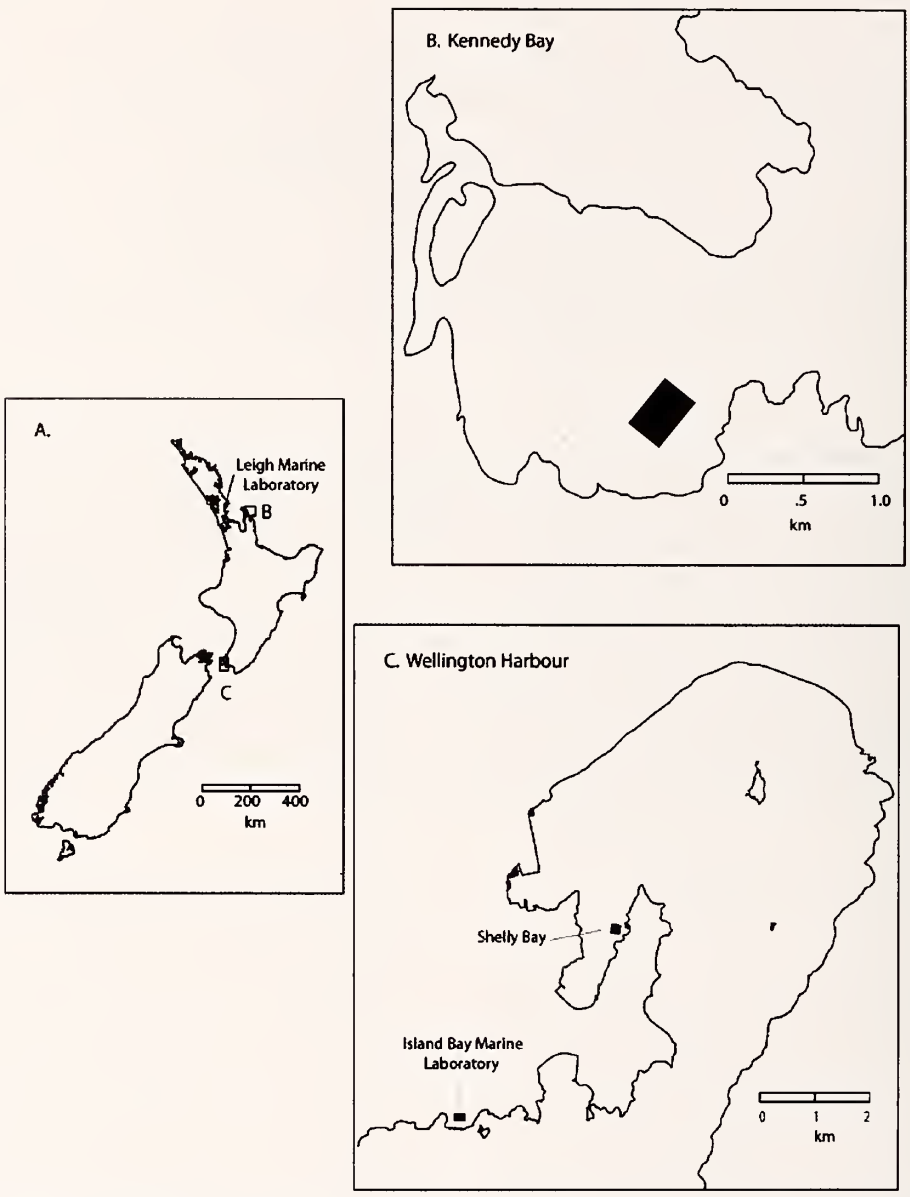

Figure 1. Maps showing the location of the two study populations, where geoducks were collected for reproductive analysis from June 1990 to March 2001. Black boxes in Kennedy Bay (B) and Shelly Bay (C) indicate areas where geoducks were collected.

slides was also used to quantify the reproductive development of female geoducks in both populations. The use of GSIs (wet weight and dry weight ratios) as quick and adequate descriptors of reproductive condition was also investigated. Additional information on size at sexual maturity and sex ratios in the two populations was also obtained.

MATERIALS AND METHODS

The reproductive cycle of two populations of the New Zealand geoduck, *Panopea zelandica*, was investigated using histological analysis of samples collected from Kennedy Bay, Coromandel Peninsula, and Shelly Bay, Wellington (Figure 1). Monthly samples of approximately 20 geoducks (size range 37–128 mm shell length) were collected subtidally from both populations in 5–12 m of water using SCUBA from June 1999 to March 2001.

Clams were processed within 4 hours of collection. Length (anterior-posterior axis of the right valve) was measured to the nearest millimeter using vernier calipers and whole wet-weight to the nearest 0.1 g using a Mettler electronic balance. The shell was removed, blotted with tissue paper to remove any remaining water, and weighed.

Table 1

Criteria used to stage histologically prepared slides. Adapted from Porter (1964), Ropes (1968), Anderson (1971), Goodwin (1976) and Beattie (1989).

Stage	Males	Females
Early active	Follicles small and walls thick. Follicles contain spermatogonia. Gonad volume in small and connective tissue abundant. Sperm ducts co ıtracted.	Follicle small walls thick. Follicles mainly contain oogonia and primary oocytes present. A few secondary oocytes may also be visible. Gonad volume is small and connective tissue abundant.
Late active	Follicles larger walls not as thick. Spermatogonia occupying ~⅓ the volume of the follicle restricted to lining the follicle walls. Follicle dominated by dense areas of spermatids and spermatocytes. Spermatozoa also present. Connective tissue less abundant and sperm ducts expanding.	Follicle larger, walls not as thick. Follicles dominated by secondary oocytes with fewer oogonia and primary oocytes present. Oocytes elongated in shape. Connective tissue less abundant.
Ripe	Spermatogonia as for late active. Follicle dominated by very dense columns of spermatozoa with tails pointing into the lumen. Spermatids and spermatozoa occupy less follicle volume. Gametes occupy nearly all the gonad volume. Very little connective tissue. Sperm ducts fully expanded.	Follicle are large and walls thin containing ova often lying free in the lumen. there is little ovogenic activity within the follicle except for a few primary and secondary oocytes. Ova are usually spherical in shape. Very little connective tissue.
Partially spawned	Follicle smaller and walls still thin. Spermatozoa less abundant. Center of the lumen often appears empty. Spermatogonia intrude farther into the follicle although no more abundant than in the previous stage. Spermatids and spermatocytes less dense but still fairly common. Little connective tissue, and sperm ducts still expanded. Spermatozoa often visible in ducts.	Follicles are very large and walls still thin. There are usually large spaces within the lumen, although free ova are still frequent within lumen of the follicle. There are still mature oocytes present. Very little connective tissue.
Spent/Resorbing	Follicle small and walls are thick. Few unspawned spermatozoa remain. Connective tissue more abundant but less so than in early active stage. Sperm ducts contracting. All gametes will be resorbed and only sperm ducts visible.	Follicles small and walls thick. Few oocytes and ova remain. Connective tissue more abundant but less so than in early active stage. All gametes will be eventually be resorbed.

The tissue (including siphons, gills, mantle, and visceral mass) was weighed to give total wet tissue weight. The visceral mass (with associated gonad, gut, and attached foot) was then excised, weighed, and fixed in Bouin's solution for a period of no less than 3 days. The remaining tissue was placed in a foil tray of known weight and dried in an oven for 3 days at 60°C. Dry tissue weight was calculated by subtracting tray weight from the combined weight of the tray plus dried tissue.

Samples were dehydrated using a graded ethanol series, blocked in paraffin wax, and sectioned at 7 μm. One lateral section was taken near the front of the viscera (where most of the gonadal material was located) for all clams collected. All sections were stained with hematoxylin and counterstained with eosin. The histologically prepared slides were examined using a compound microscope at ×4, ×10, and ×40 magnification. Gonads from both male and female clams were placed into five qualitative categories adapted from Porter (1964), Ropes (1968), Andersen (1971), Goodwin (1976), and Beattie (1989): early active, late active, ripe, partially spawned, and spent/resorbing (Table 1; Figures 2A–J). The gonadal state of each clam was described as one of the five stages based on the most dominant stage present in 10 haphazardly selected follicles from each sample.

For female geoducks, monthly mean oocyte diameters (± SD) and monthly mean number of eggs per follicle (± SD) were determined using video image analysis (Image Tool Version 2.0; UTHSCSA 1997). The diameters of all oocytes within five haphazardly selected follicles from each slide were measured for all female clams sampled in each month. Only oocytes with visible nuclei were measured, but all oocytes present were counted.

GSIs used as quick determiners of gametogenic development and as gross indicators of spawning events were calculated from the wet-weight and dry-weight measures determined above. GSIs were calculated for each monthly sample collected from both populations. Indices calculated included: gonad weight:whole wet weight, gonad weight:wet tissue weight, gonad weight:dry tissue weight (with gonad removed), and gonad weight:wet shell weight. All indices are expressed as percentages.

Two condition indices (wet tissue weight:wet shell weight, and dry tissue weight:wet shell weight) were also calculated for both sites to confirm that any increase or decrease in condition was due to changes in reproductive

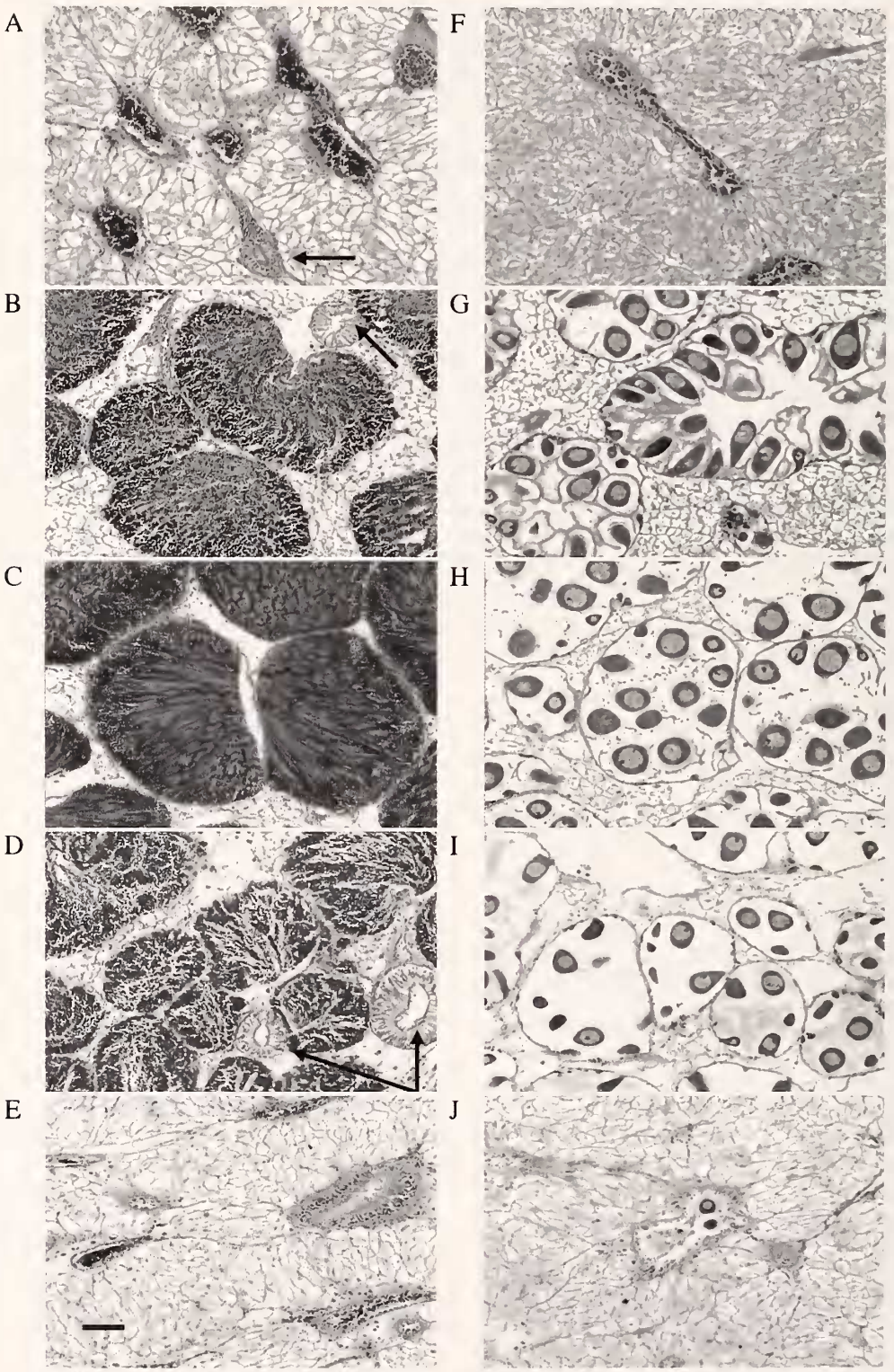

Figure 2. Photomicrographs of reproductive stages; Males: (A) early active, (B) late active, (C) ripe, (D) partially spawned, and (E) spent/resorbing; Females: (F) early active, (G) late active, (H) ripe, (I) partially spawned, and (J) spent/resorbing. Scale bar = 100 μm. Arrows indicate position of sperm ducts.

condition and not caused by changes in tissue condition. Gonad weight was excluded from both these indices (i.e., tissue weight is for everything minus the viscera). The dry tissue weight index was chosen as the use of dry tissue weights eliminates the bias due to water content fluctuations and probably represents the best static condition index available (Lucas & Beninger, 1985).

The ratio of males to females was determined from microscopic examination of the histological slides for both the Wellington and Kennedy Bay populations. Clams were deemed sexually mature if gametes were present. A Chi-squared goodness of fit test ($\alpha = 0.05$) was used to test the hypothesis that there was an equal representation of males and females in each population. Clams were also examined for any evidence of hermaphroditism. Size at sexual maturity was also assessed from microscopic examination of the histological slides by correlating the state of development of a gonad with the size (shell length) of the animal from which it was dissected.

RESULTS

Reproductive Cycle

The gametogenic development and spawning of geoducks in both Kennedy Bay and Shelly Bay were synchronous between sexes (Figures 3, 4). However, there were differences in the length and timing of the reproductive stages and in the overall length of the seasonal reproductive cycle between localities despite gametogenic development starting around the same time of year (May–June) for both populations.

All clams collected from Kennedy Bay in June 1999 (early winter) were in an early active condition, with late active clams dominating by October (spring). By late November, partially spawned and spent clams prevailed, with all clams appearing spent by January 2000 (summer). Following spawning, clams went through a period of resorbing all their residual gametes. During 2000, early gametogenic development began in May (late autumn) and lasted until August (winter) when late active individuals dominated the population (Figure 3). The majority of clams were in a ripe condition by September/October (spring). The spawning season began in October, and by the end of the month nearly all clams appeared partially spent. By January/February 2001 (summer) most geoducks were completely spent. Although fewer samples were collected during the 1999/2000 reproductive season due to poor weather, reproductive development appeared to follow a similar pattern to the 2000/2001 season.

Gametogenic development of geoducks in Shelly Bay began about the same time as that in Kennedy Bay (May/June) (Figure 4). However, the development of gametes was slower, and the entire reproductive cycle lasted until autumn the following year; approximately 3 months longer than in Kennedy Bay. Gonads dominated by early active stages were prevalent up until November 1999

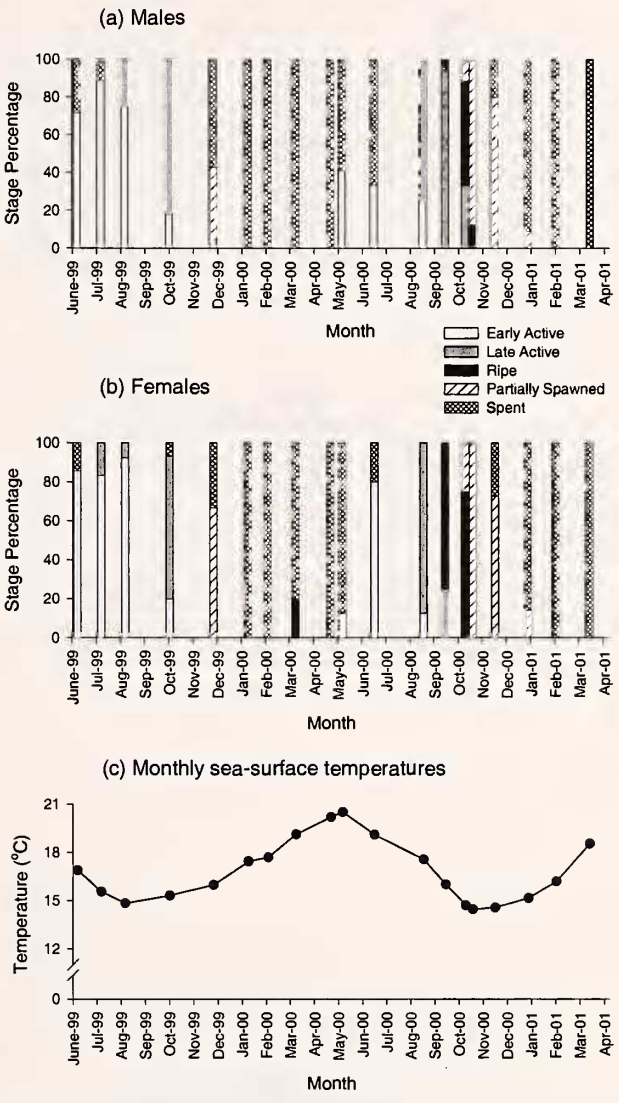

Figure 3. Histograms showing the reproductive cycle of *P. zelandica* in Kennedy Bay for (a) males and (b) females determined from analysis of histological sections, (c) monthly mean sea-surface temperatures (data from NIWA). Arrows indicate the start of the spawning season.

(early summer) after which late active clams dominated the population. Clams continued to develop through to February (late summer) 2000 when the majority appeared in a ripe or late active state. Spawning began in February with the appearance of partially spawned individuals, and continued through until April (autumn) when all clams appeared in a spent condition except for a single ripe male. The 2000/2001 spawning season was similar to 1999/2000, although partially spawned or spent individuals occurred a month later than observed in the previous season; February 2000 and March 2001, respectively.

During late autumn (the onset of gametogenic development), sea-surface temperatures were at their highest,

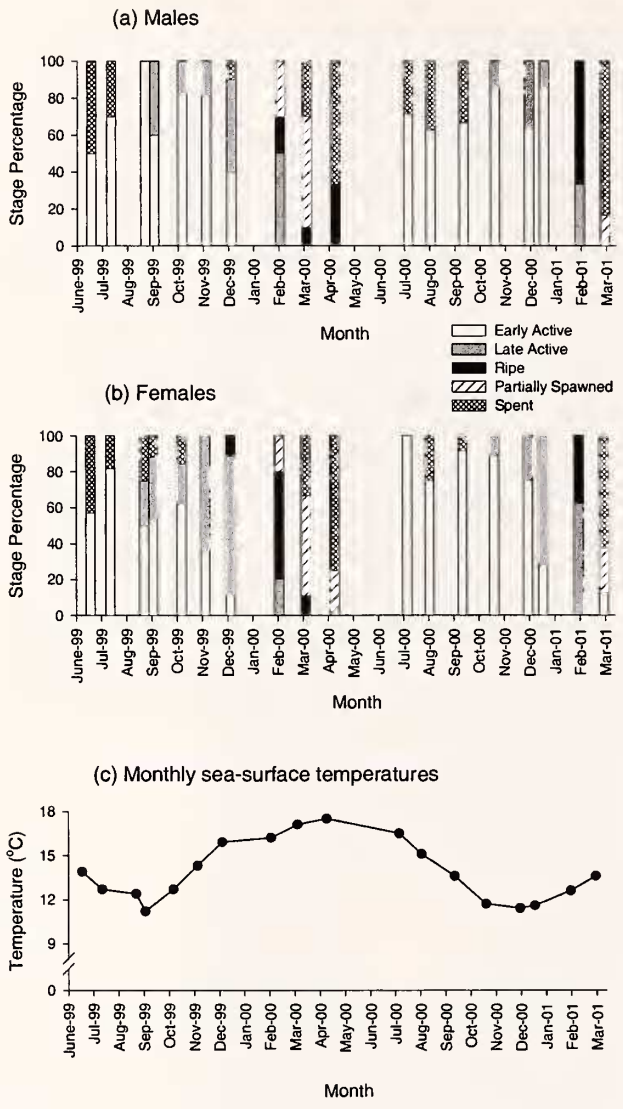

Figure 4. Histograms showing the reproductive cycle of *P. zelandica* in Shelly Bay for (a) males and (b) females determined from analysis of histological sections; (c) monthly mean sea-surface temperatures (data from NIWA). Arrows indicate the start of the spawning season.

and gametogenesis continued as temperatures fell (Figures 3, 4). Both populations began spawning when temperatures were ~ 15°C, except for the 2001 spawning season in Shelly Bay where spawning began at ~ 13°C. In Kennedy Bay this was the period when water temperatures were at their lowest (Figure 3), whereas in Shelly Bay they had been rising for a couple of months (Figure 4).

Oocyte Diameters

Oocyte diameters in both Kennedy Bay and Shelly Bay ranged from 6–64 μm (Figures 5, 6). Frequency histograms of oocyte diameters for both populations confirm the patterns observed in the qualitative staging of reproductive development.

In Kennedy Bay, small primary oocytes (median size of 13.0 μm) dominated through June and July 1999 (winter) (Figure 5). Increased gametogenic activity was observed during August and September (late winter/early spring) with lots of primary and secondary oocytes, and some ova present (median size of 30.8 μm). Spawning was evident in the November sample with few oocytes of any size remaining. Only a very few small oocytes remained by January 2000 (summer). A similar pattern of development was observed in the following 2000/2001 spawning season.

During 1999, development of oocytes in Shelly Bay began in June (winter) with the appearance of primary oocytes (median size of 10.6 μm) (Figure 6). Development continued through the following months with secondary oocytes and some ova apparent from September (spring) (median size of 40.3 μm). Spawning was observed in February 2000 (summer) and by March (early autumn) very few oocytes remained. Primary oocytes were present again in July 2000 (winter), indicating the beginning of reproductive development again. Development continued as for the previous year with large secondary oocytes and ova dominating during January 2001 (summer). Very few oocytes remained by March (autumn) indicating that spawning had occurred.

In both populations, mean oocyte diameters increased as gametogenesis progressed with high oocyte diameter values associated with the onset of spawning in both populations: during January 2000 (summer) and February 2001 (later summer) in Shelly Bay, and November 1999 and October 2000 (spring) in Kennedy Bay (Figure 7). However, the largest monthly mean diameters generally occurred in those months immediately following the beginning of spawning. The high value occurring in Kennedy Bay during March 2000 was due to the appearance of a single ripe female. The remaining females in the sample contained very few residual eggs. The large standard deviations observed for both populations, for all months, indicates the large variability in oocyte diameters present in any month. Shelly Bay had higher peak monthly mean oocyte diameters in both spawning seasons, excluding the Kennedy Bay sample collected during March 2000.

Monthly mean number of eggs/follicle suggests that small levels of spawning may have occurred earlier than observed in histological stagings (Figure 8). In Kennedy Bay, peak values were reached in early October 1999 (spring) and in August 2000 (winter) and decreased thereafter. This was 1–2 months earlier than spawning was inferred from the histological stagings (Figure 3). In Shelly Bay, the highest values occurred in October 1999 (spring) and remained high until February 2000 (summer), when they decreased with the onset of spawning in

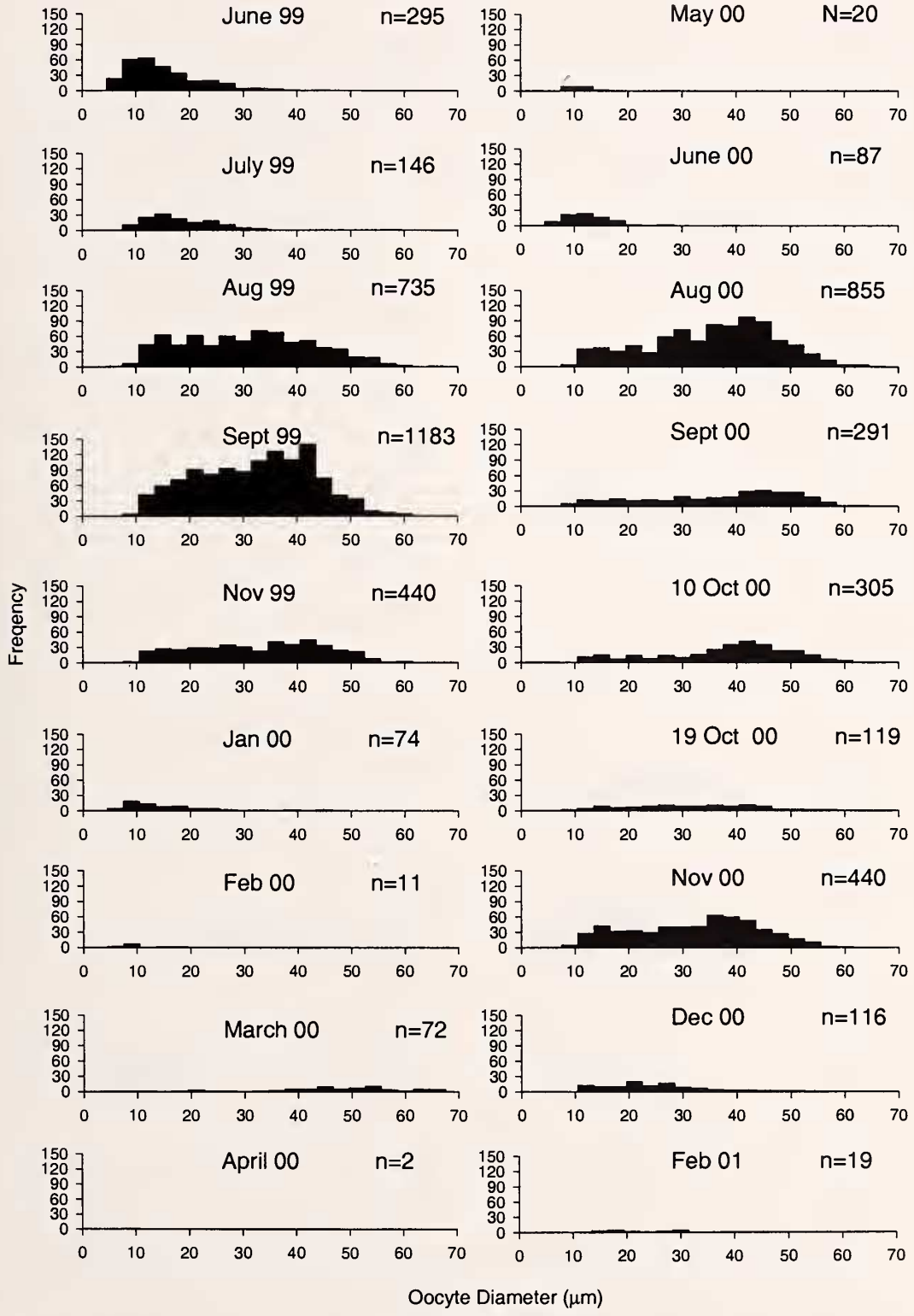

Figure 5. Frequency histograms for all oocyte diameters measured within five haphazardly selected follicles from all females collected from Kennedy Bay.

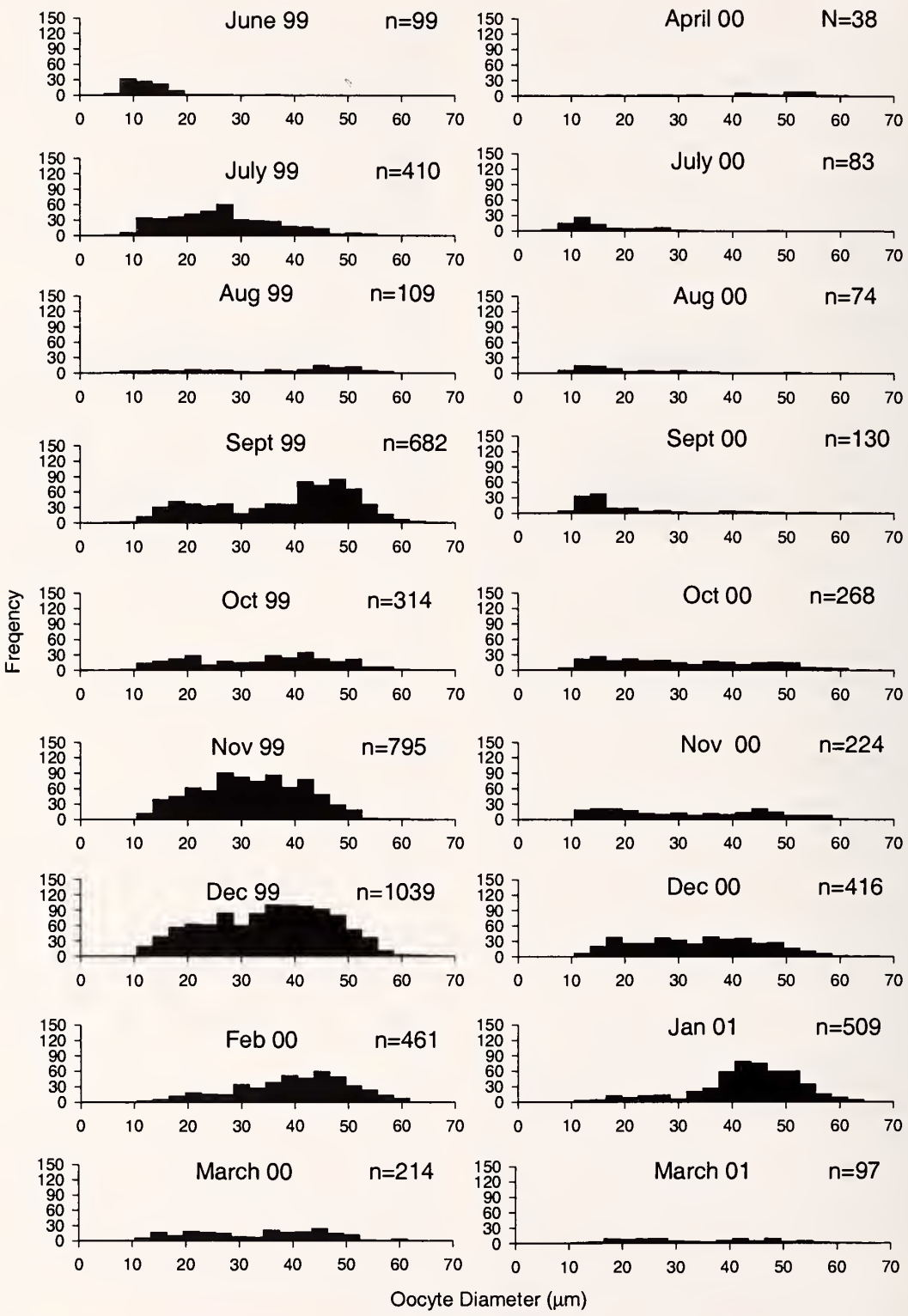

Figure 6. Frequency histograms for all oocyte diameters measured within five haphazardly selected follicles from all females collected from Shelly Bay.

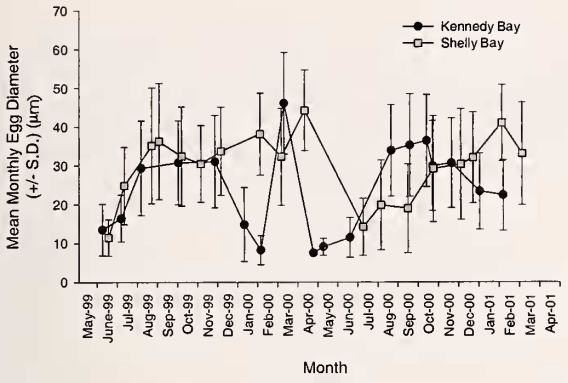

Figure 7. Seasonal variation in mean monthly oocytes diameters (± SD) for Kennedy Bay and Shelly Bay from June 1999 to March 2001. Oocyte diameters from five haphazardly selected follicles from each female collected within each month were pooled to calculate monthly values.

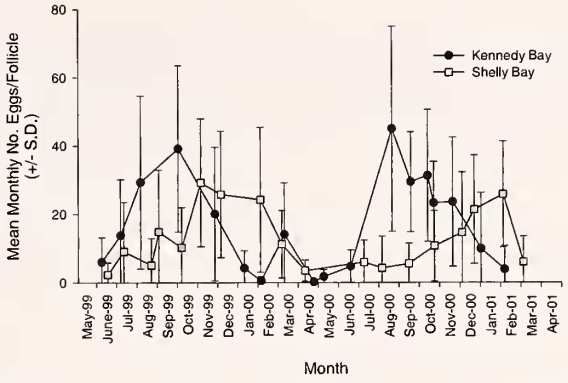

Figure 8. Seasonal variation in mean monthly number of eggs/follicle (± SD) for Kennedy Bay and Shelly Bay from June 1999 to March 2001. The number of eggs/follicle from five haphazardly selected follicles from each female collected within each month was used to calculate monthly values.

March (autumn) (Figure 4). During the following season, numbers peaked in February and again decreased when spawning began in March. Kennedy Bay had higher peak monthly mean number of eggs/follicle during both spawning seasons. Again, there was a large amount of variability in the monthly mean number of eggs/follicle.

GSIs and Condition Indices

All GSIs followed similar patterns that appeared to be closely related to the reproductive development seen in the histologically prepared slides for both populations (Figure 9). Only the dry weight GSI and condition index are presented as these proved to be the most sensitive to changes in reproductive development. The patterns were less obvious in the whole weight GSI. This was probably due to the retention of water in the internal cavity of the geoducks slightly masking any pattern in the GSI. GSI values were at their lowest prior to the onset of gametogenic development. Indices began rising in May/June (autumn/winter). Values in both bays peaked prior to the spawning events inferred from the histological stagings. In Kennedy Bay, there was also a peak in the GSIs during February (summer) 2001 suggesting a secondary summer spawning. However, this was not evident in the qualitative stagings. GSIs began falling following the beginning of the spawning season.

The dry tissue weight condition indices for both Kennedy Bay and Shelly Bay do not appear to follow any distinct pattern, remaining fairly constant throughout the sampling period (Figure 9). The pattern was the same for wet tissue weight index, (data not presented), although there was more variability. Again, this was probably due to the retention of water within the geoducks.

Sex Ratio and Size at Sexual Maturity

Overall, there were significantly more males than females (ratio 1.5:1) collected from Kennedy Bay, mainly due to a large cohort of male clams (< 90 mm) (Figure 10; Table 2). In Shelly Bay there were significantly more females than males (ratio 1.3:1) (Figure 11; Table 2). The smallest geoducks were collected from Shelly Bay (< 80 mm) were also predominately male although they were much less abundant than in Kennedy Bay.

The size range and mean length of male, female, and undifferentiated clams were similar for both Kennedy Bay and Shelly Bay. Male geoducks collected in Kennedy Bay ranged in size from 52–121 mm in shell length, females from 70–129 mm, and undifferentiated clams from 31–70 mm in shell length (Figure 10; Table 2). Shell lengths of geoducks collected from Shelly Bay ranged from 57–121 mm for males, 75–120 mm for females, and 47–67 mm for unsexed clams (Figure 11; Table 2). The mean length of females was higher than males in both

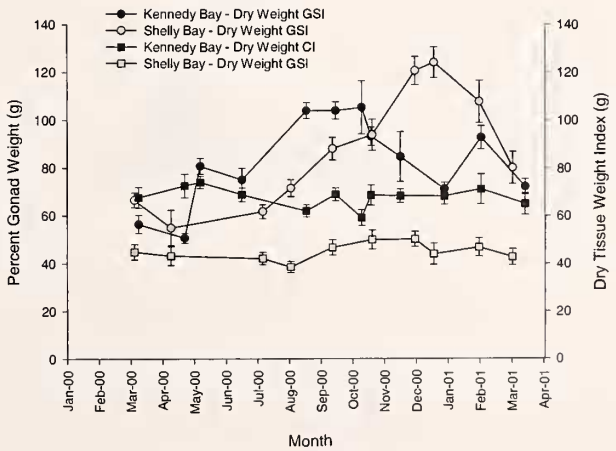

Figure 9. Seasonal variation in the dry weight GSI (gonad weight: dry tissue weight) and dry weight condition index (dry tissue weight:wet shell weight) for geoducks in Kennedy Bay and Shelly Bay from February 2000 to March 2001.

Table 2

Range, mean length (±SD) and total number of undifferentiated (U), male (M) and female (F) clams collected from Kennedy Bay (KB) and Shelly Bay (SB) between June 1999 and March 2001. χ^2 test for sex ratios differing from 1:1 ($\chi^2_1 = 3.84$ at $\alpha = 0.05$). Significant values in bold.

	Range (mm)			Mean length (±SD)			Total no.			
Site	U	M	F	U	M	F	U	M	F	*P*-value
KB	31–70	52–123	70–128	56 (7.6)	95 (17.27)	108 (11.1)	27	235	153	**0.0001**
SB	47–67	61–121	75–120	55 (8.6)	96 (11.7)	100 (8.5)	4	167	210	**0.03**

Kennedy Bay and Shelly Bay. In both population, males matured at a smaller size than females (Figures 10, 11; Table 2). In Kennedy Bay, most male geoducks appeared to mature at around 70 mm, whereas in Shelly Bay males appeared to mature at approximately 60 mm. Females in Kennedy Bay appeared to mature at ~100 mm, with females in Shelly Bay maturing at ~ 80 mm.

DISCUSSION

Goodwin (1976), and Sloan & Robinson (1984) found slight differences in the seasonal pattern of gametogenesis and spawning between male and female North American geoducks, *Panope abrupta,* in Puget Sound, Washington and southern British Columbia, respectively. Andersen (1971), however, found no such differences between male and female geoducks in Hood Canal, Washington State. In our study, reproductive development and spawning was synchronous between the sexes for *P. zelandica* in both Kennedy Bay and Shelly Bay, and appeared to be related to changes in water temperatures.

Although gametogenic development started around the same time of year (late autumn-early winter), there were differences in the length of both gametogenic development and spawning between the populations. Spawning in Kennedy Bay began in October/November (spring), a pattern similar to that observed for populations of *P. abrupta* from southern British Columbia (Sloan & Robinson, 1984), Puget Sound (Goodwin, 1976), and Hood Canal (Andersen, 1971) in Washington. However, spawn-

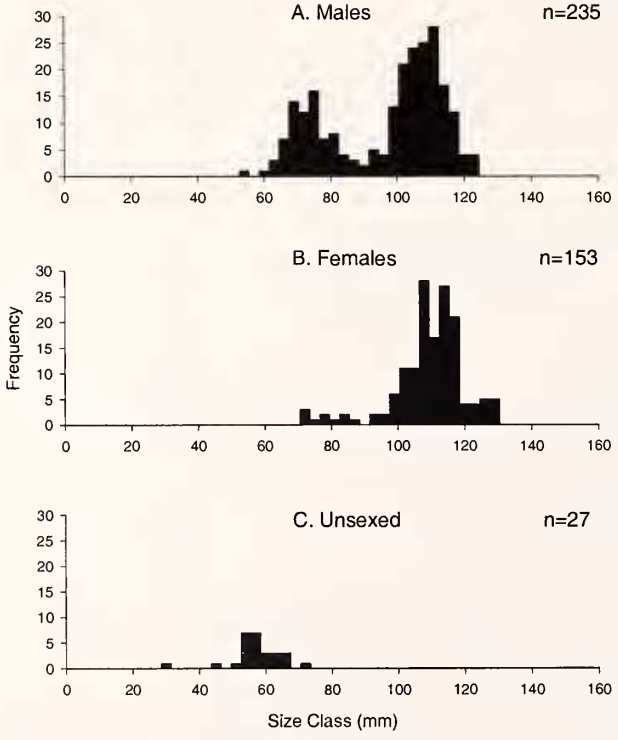

Figure 10. Length frequency distributions of male, female, and unsexed geoducks collected for histological analysis in Kennedy Bay from June 1999 to March 2001.

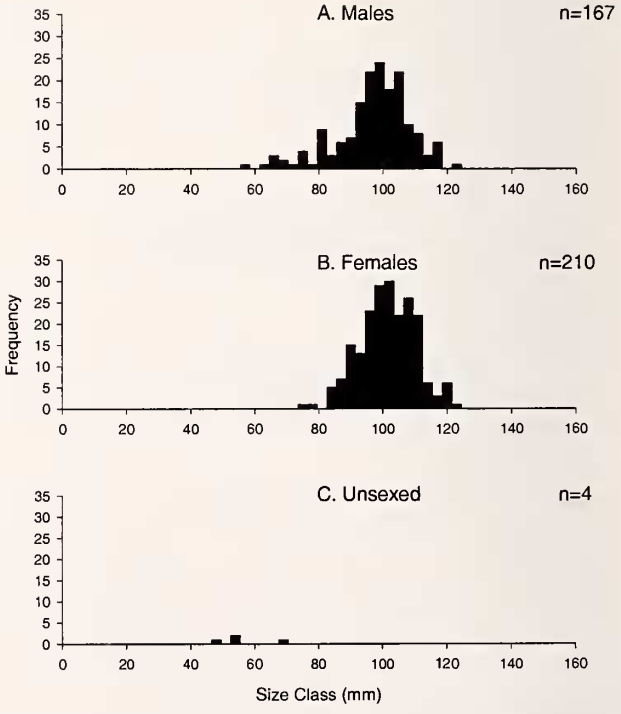

Figure 11. Length frequency distributions of male, female, and unsexed geoducks collected for histological analysis in Shelly Bay from June 1999 to March 2001.

ing in Shelly Bay occurred during February/March (late summer). This is in agreement with a preliminary study by Breen et al. (1991) who suggested that *P. zelandica* in Golden Bay, Nelson, which is on a similar latitude to Wellington Harbour, spawn during summer and autumn.

Latitudinal gradients in the timing of gametogenic development, spawning, and in the number of spawning events in a reproductive season are common among clam species that exist over a broad geographical range. A similar pattern of early gonad ripeness and spawning patterns as that described here for southern latitudes is well documented for clam populations in North America (Porter, 1964; Ropes & Stickney, 1965; Keck et al., 1975; Sastry, 1979; Manzi et al., 1985; Eversole, 1989; Heffernan et al., 1989; Kanti et al., 1993). Temperature is often considered the most important factor in the timing of spawning (Keck et al., 1975; Eversole, 1989; Hadfield & Anderson, 1988; Heffernan et al., 1989) with spawning usually commencing following either an increase to a specific temperature (e.g., Brousseau, 1978) or a relative change in temperature (e.g., Ropes, 1968). Sloan & Robinson (1984) suggested that *P. abrupta* may spawn during summer in response to increases in ambient seawater temperatures. Both populations of *P. zelandica* spawned between 15–17°C when water temperatures were increasing. However, in Kennedy Bay, this was during a period when sea-surface temperatures were at their lowest, while in Shelly Bay they were near their highest. In both instances, these were not periods of rapidly increasing or declining temperatures, suggesting that spawning in these two populations is induced by an increase to a specific temperature rather than by any relative changes in temperature.

Many authors have used analysis of oocyte diameters to quantify gametogenic development and spawning events. Close relationships were found between oocyte diameter measurements and the gametogenic cycles of *Spisula solidissima similis* in St. Catherines Sound, Georgia (Kanti et al., 1993), and the cockle, *Laevicardium elatum,* in Mexico (Villalejo-Fuerte et al., 1996). Xie & Burnell (1994) found length frequency histograms supported qualitative data on the reproductive cycles for both *Tapes philippinarum* and *T. decussatus* on the south coast of Ireland. Although studies that have employed quantitative analysis indicate that periods of maturation and spawning tend to coincide with maximum oocyte diameter values, the relationship between oocyte diameters and the remainder to the reproductive cycle remains unclear (e.g., Heffernan & Walker, 1989; Hesselman et al., 1989; Gribben et al., 2001). Quantitative analysis of oocyte diameter frequency histograms, monthly mean egg diameters, and monthly mean number of eggs/follicle all appeared to be good quantitative descriptors of the reproductive development and spawning for *P. zelandica,* and closely follow the patterns observed in the qualitative stagings of *P. zelandica* in both Kennedy Bay and Shelly Bay. However, consideration of monthly mean number of eggs/follicle values suggests that the spawning season may start earlier than that observed in the histological stagings. The oocyte diameter frequency histograms for Kennedy Bay and Shelly Bay both have small numbers of large oocytes and ova present 2–3 months prior to the onset of the main spawning season observed and it may be these eggs that are being spawned.

GSIs are generally regarded as insufficient descriptors of reproductive development (e.g., Eversole et al., 1980; Heffernan & Walker, 1989; Hesselman et al., 1989; Gribben et al., 2001). However, Fritz (1991) found that changes in dry tissue weight reflected the gametogenic cycle of *Arctica islandica* off New Jersey, as did Ansell et al. (1980) for *Donax trunculus* on the Algerian coast and Eversole et al. (1984) for *M. mercenaria* in South Carolina. Several other authors have reported correlations between drops in peak GSI values and spawning observed in qualitative stagings (e.g., Feder et al., 1979; Villalejo-Fuerte et al., 1996). All the GSIs calculated for *P. zelandica* in both Kennedy Bay and Shelly Bay correlate well with the development of the reproductive season seen in the qualitative stagings. Although the dry tissue weight GSI appears to be the most sensitive to changes in the reproductive cycle, it takes the longest to compile. Aquaculturalists or fisheries managers wanting to quickly assess the reproductive state of potential *P. zelandica* broodstock would be just as well served using the whole wet weight, wet tissue weight or wet shell weight GSI. However, Lucas & Beninger (1985) and Villalejo-Fuerte et al. (1996) noted that wet tissue weight indices should be used with caution as bivalves in poor condition can compensate organic loss with water uptake.

The possibility remains that changes in GSIs were due to seasonal changes in tissue condition and not a result of changes in reproductive development. Both the dry and wet tissue weight condition indices changed very little over the duration of the study, although the wet tissue index was more variable. This has two important implications. Firstly, it confirms that the changes in GSIs were due to the development of reproductive products and not due to any seasonal changes in tissue weight. Secondly, unlike other bivalves (i.e., clams, oysters, and mussels) that can only be harvested at limited times of the year, the quality of meat from harvested geoducks remains constant.

A review of the sex ratios of clams by Eversole (1989) found that they rarely differ from 1:1. However, several authors note unequal sex ratios in some clam species (e.g., Eversole, 1989; Ropes et al., 1984; Rowell et al., 1990). Andersen (1971) found unequal sex ratios for the North American geoduck, *P. abrupta,* from Hood Canal, Washington, while Goodwin (1976) found an overall sex ratio of 1:1 for *P. abrupta* in Puget Sound Washington. The difference in sex ratios between Kennedy Bay and Shelly Bay was due to the large cohort of small male geoducks present in Kennedy Bay (< 90 mm). If this

cohort is removed, the sex ratios are not significantly different than one ($P = 0.42$). However, all the small geoducks (< 70 mm) found in Shelly Bay were male.

The dominance of small size classes by male clams has been reported for several clam species including *P. abrupta* (Andersen, 1971), the ocean quahog, *Arctica islandica* (Rowell et al., 1990), and the hardshell clam, *M. mercenaria* (Eversole et al., 1980; Eversole, 1989). It is possible that geoducks are protandric like *M. mercenaria* (Eversole et al., 1980; Eversole, 1989). Andersen (1971) found no evidence of protandry in the North American geoduck, and suggested that the presence of sperm ducts in adult males is a defining characteristic of their sexuality. However, *P. zelandica* goes through a period of complete resorption of gametes post spawning. It may be possible that small males resorb these sperm ducts as well as residual sperm during this period and then develop as females. Alternatively, females may grow faster than males, maturing at the same age but a larger size, as occurs with *A. islandica* (Rowell et al., 1990). If females grew at the same rate and matured at a larger size, more undifferentiated clams should have been evident in the smaller size classes. However, it is impossible to determine which theory is appropriate for *P. zelandica* without knowing the size-age relationships for males and females. Andersen (1971) did not present these sorts of data for *P. abrupta*.

According to Eversole (1989), sexual maturity could be a function of size (shell length), age, or some interaction between size and age. Evidence suggests that *P. abrupta* matures prior to 5 years of age (Andersen, 1971; Sloan & Robinson, 1984). Andersen (1971) found that male *P. abrupta* from Hood Canal, Washington, matured at a size of > 45 mm and females at a size of > 85 mm. These patterns are similar to those found in this study, with male *P. zelandica* maturing before females in both populations. However, both male and female geoducks from Shelly Bay mature at a smaller size than those in Kennedy Bay. Either geoducks in Shelly Bay are maturing at a younger age than those in Kennedy Bay, or they are maturing at the same age but have slower growth rates, possibly due to the cooler water temperatures in Wellington Harbour. Again, this is difficult to assess without knowing the growth rates and the relationship between size and age for *P. zelandica* in both populations. Breen et al. (1991) suggested that *P. zelandica* taken from Golden Bay, Nelson matured at age 5 years or earlier based on the number of internal rings observed in shell cross-sections. However, whether or not the rings they counted were annuli was not validated.

Aquaculture is becoming an increasingly important part of the commercial development of *P. abrupta* in North America (e.g., Beattie & Goodwin, 1992; Roberts & Shuman, 1989; Beattie, 1992; Beattie & Blake, 1999) and the hatchery culture of *P. abrupta* is already well developed (Beattie, 1992; Beattie & Blake, 1999). As there is currently no known natural supply of spat, the aquaculture of *P. zelandica* in New Zealand is going to be reliant on the production of hatchery-reared spat. This study has shown that potential broodstock from any population are ripe for only a short period of time. However, given the latitudinal gradients in reproduction, ripe broodstock should be available over an extended period as different populations mature, thus minimizing the costs of conditioning geoducks out of season. The data presented here also suggests that the use of GSIs may be of use as quick and easy indicators of the reproductive state of broodstock.

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